STUDIES ON THE LIFE HISTORY OF ANISOPORUS MANTERI HUNNINEN AND CABLE, 1940 (TREMATODA: ALLOCREADIIDAE)

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Introduction

In August, 1939, the authors discovered a new cotylomicrocercous cercaria emerging from the marine snail, *Mitrella lunata* (Say) collected at Waquoit Bay, Cape Cod, Massachusetts. During the summer of 1940, it was found that this cercaria penetrated marine amphipods and developed into progenetic metacercariae of a new species of *Anisoporus,* for which the name *Anisoporus manteri* was proposed in a preliminary abstract (Hunninen and Cable, 1940).

The genus *Anisoporus* was erected by Ozaki (1928) to contain *A. cobraeformis* from the intestine of *Diacocus petersoni.* Two other species of *Anisoporus* from marine fishes have been described by Manter (1940),—*A. eucinostomi* and *A. thyrinopsi* which is described tentatively, being possibly a developmental stage of *A. eucinostomi. Anisoporus* possesses a small accessory sucker anterior to the acetabulum, thereby differing from the closely related genera *Opecoelus* and *Opegaster.*

There has been considerable difference of opinion concerning the taxonomic significance of anal openings such as those found in *Anisoporus, Opecoelus, Opegaster* and several other genera of digenetic trematodes. Ozaki (1925) regarded anal openings as fundamental characters and accordingly proposed the family Opecoelidae to include the genera *Opecoelus* and *Coitocaecum.* Later (1928), he placed the new genera *Anisoporus* and *Opegaster* in the Opecoelidae but removed *Coitocaecum,* making it the type of a new family, Coitocaecidae. In the same paper, he also erected the family Diploproctodaeidae, with *Diploproctodaeum* La Rue as type genus and included two new species of the new genus *Diploporus.* Odhner (1928) erected the genus *Opecoeloides* and expressed the opinion that *Opecoelus* and *Opecoeloides,* because of their resemblance to *Podocotyle,* were aberrant allocreadiids. Ozaki (1929) reaffirmed his belief that anal openings were fundamental

[1] This work was assisted by a grant-in-aid to the senior author from the Society of the Sigma Xi.

characters. Stunkard (1931) has reviewed the literature concerning trematodes with anal openings and expressed the opinion that these structures have arisen independently in several families and are not of great taxonomic importance. He stated that the members of Ozaki's families Opecoelidae and Coitocaecidae might well be regarded as a subfamily, Opecoelinae, of the family Allocreadiidae. La Rue (1938) concludes that anal openings have little more than specific or generic value at the most in the taxonomy of digenetic trematodes.

The described species of freshwater and marine cotylomicrocercous cercariae and the life histories of trematodes known to have this type of larva are listed by Cable (1938, 1939) and Dobrovolny (1939*a*).

Materials and Methods

Material was collected in abundance from Waquoit Bay, near Woods Hole, Massachusetts, and studied mostly while living. Stained whole mounts and serial sections of certain stages were prepared, using conventional technics. Cercariae were studied with the aid of neutral red and Nile blue sulphate supravital stains. The morphology of the metacercaria and adult was observed in specimens from both naturally and experimentally infected amphipods and fishes. Amphipods were infected experimentally by placing them with infected snails in finger bowls which were covered with cheese-cloth and placed in slowly running sea water. All measurements given below are in millimeters. Eleven adults were measured as stained whole mounts; all other measurements were made on living material under light cover-glass pressure.

Observations

Experimental Proof of the Life History

Technical difficulties and brevity of the season made it impractical to rear parasite-free amphipods and fishes in the laboratory. For this reason, proof of the life history is based on the fact that penetration of the cercariae into amphipods could be induced at will and subsequent development followed as a continuous process from very young to mature, progenetic metacercariae with eggs in the uterus and discharged from the body into the surrounding cystic fluid. Amphipods exposed to cercariae in the laboratory usually contained a larger number of metacercariae and always showed a much higher incidence of infection than did amphipods collected in the field. Experimental infections superimposed on natural infections could be detected by differences in cyst size.

Fishes were infected experimentally by feeding them large numbers of amphipods. Worms recovered from experimentally as well as naturally infected fishes were little further developed than were the progenetic metacercariae.

Description of Stages in the Life Cycle

Adult (Figs. 7–10)

Specific Diagnosis.—Small, elongate worms with characters of the genus *Anisoporus*. Total length 0.74–2.32 (average 1.54); width 0.28–.46 (0.35). Oral sucker width 0.07–.14 (0.114); acetabulum in anterior third of body, 0.12–.17 (0.144) wide, provided with three anterior and two posterior papillae; sucker ratio approximately 2 : 2.5. Prepharynx very short, pharynx spherical, 0.07–.11 (0.09) in diameter; esophagus length 0.07–.18 (0.124); ceca extend almost to posterior end of body, uniting with excretory bladder, the excretory pore functioning as an anal opening. Testes tandem, in posterior half of body; anterior testis 0.13–.2 (0.16) wide and 0.07–.16 (0.12) long; posterior testis 0.14–.2 (0.18) by 0.07–.17 (0.13); cirrus sac lacking. Ovary ovoid, median, anterior to testes, 0.09–.14 (0.11) wide and 0.05–.12 (0.09) long; seminal receptacle lacking; Laurer's canal present. Uterus anterior to ovary, with few coils; vitelline follicles large, beginning just behind acetabulum and extending to posterior end of body, the lateral fields coalescing posteriorly; two accessory vitelline ducts extending transversely, one anterior to ovary, the other posterior to testes. Eggs 0.062–.068 (0.065) by 0.035–.04 (0.038). Excretory vesicle sac-shaped; excretory formula $2[(2+2)+(2+2)]$.

Hosts.—Northern pipefish, *Syngnathus fuscus* Storer; flounder, *Paralichthys dentatus* (Linnaeus); sand dab, *Hippoglossoides platessoides* (Fabricius); four-spined stickleback, *Apeltes quadracus* (Mitchill) and the killifishes, *Fundulus heteroclitus* (Linnaeus) and *F. majalis* (Walbaum).

Locality.—Waquoit Bay, Cape Cod, Massachusetts, U. S. A.

Type Specimens.—Holotype No. 36781 and Paratype 36782, Helminthological Collection, U. S. National Museum.

The body is elongate, tapering slightly at both ends. The cuticula is aspinose and is modified near the anterior end of the body to form small papillae (Fig. 9), each set with a very delicate "hair." The papillae are visible only in living material.

The ventral sucker is embedded in a large, stalk-like protrusion of the body, making it very difficult to mount worms so that the sucker is not displaced to one side. This displacement always causes distortion which alters the relationships of various structures. The characteristic lobes on the margin of the ventral sucker are shown in Fig. 6. The accessory sucker (Fig. 7) is seen more distinctly in living than in fixed and stained specimens and hence may have been overlooked in species at present assigned to genera other than *Anisoporus*. It is ventral in position, about midway between the acetabular stalk and the pharyngeal level, and appears to lie slightly to the left of the midventral line. The sucker has no connection with the genital pore which lies at the posterior end of the pharynx.

The shape of the oral sucker and pharynx depends on their state of contraction, being either subspherical or slightly wider than long. The short prepharynx is evident only in extended specimens. The esophagus bifurcates at the level of the acetabulum. In the living worm, a patch of tiny papillae is seen where the ceca join the bladder. These papillae are in the bladder proper and in sections resemble the inner processes of the muscle cells in *Ascaris*. They are especially noticeable during rhythmic contractions of the posterior end of the body.

The testes are intercecal; in moderately contracted worms, they lie close together, one behind the other, are definitely wider than long, and without notches or lobes. In extended specimens, the testes lie some distance apart and are spherical in shape. The vasa efferentia extend anteriorly and unite to form a very short vas deferens. The seminal vesicle is long, beginning well behind the acetabular level, almost as far back as the ovary in contracted specimens. The vesicle is continuous with a narrow, delicate ejaculatory duct which is difficult to trace as it approaches the genital pore.

The ovary lies in front of and in contact with the anterior testis. From the anterior surface of the ovary, the ciliated oviduct (Fig. 10) bends abruptly to the right, extends a short distance, then turns anteriorly and is joined immediately by the Laurer's canal. The canal crosses to the left of the median line and opens dorsally. From the junction of the oviduct and Laurer's canal, the oötype and uterus extend

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Explanation of Plate I

(All figures concern *Anisoporus manteri*)

Fig. 1. Cercaria, ventral view.
Fig. 2. Stylet of cercaria, dorsal view.
Fig. 3. Metacercaria, 2-day infection.
Fig. 4. Amphipod with a moderately heavy infection with metacercariae.
Fig. 5. Metacercaria, showing excretory system and other details of structure.
Fig. 6. Ventral view of acetabulum, showing characteristic papillae.

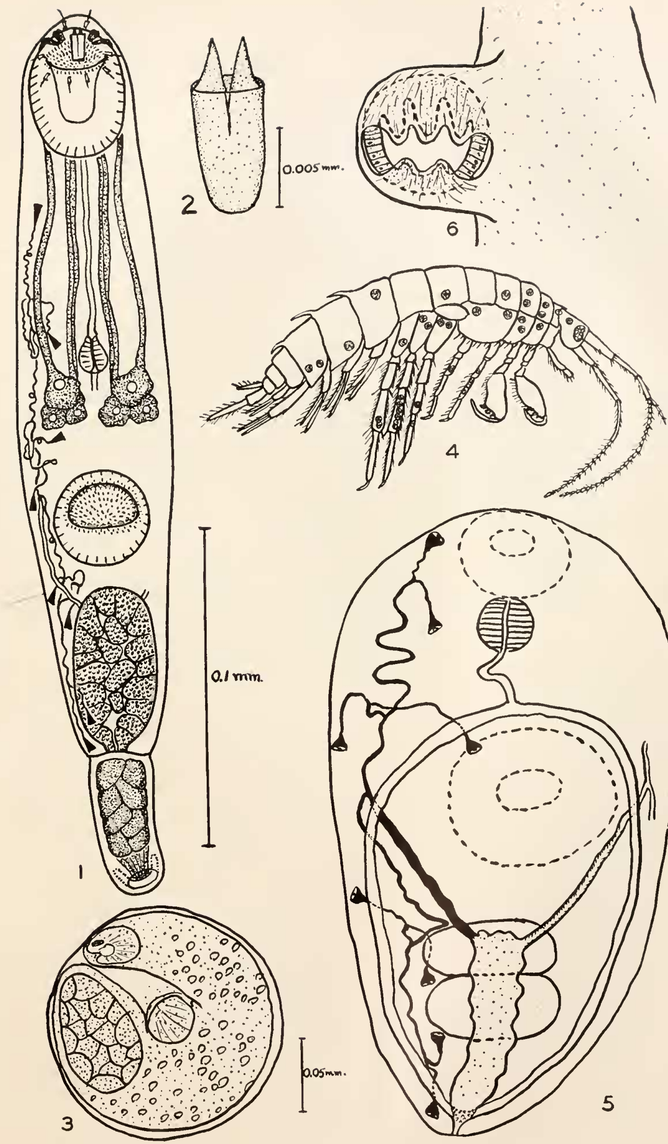

PLATE I

anteriorly as a moderately sinuous tube. The uterus usually contains only a few eggs but as many as 80 have been counted. On each side of the body, an anterior and posterior vitelline duct join to form the transverse common vitelline duct which is expanded medially to form the vitelline reservoir. This reservoir joins the oötype just posterior to Mehlis' gland. The longitudinal vitelline ducts are connected by a pair of transverse accessory ducts (Fig. 7), one anterior to the ovary, the other posterior to the testes. These transverse ducts are clearly visible only when filled with vitelline material and may be overlooked when empty.

The excretory vesicle is a long, simple tube with small cells scattered over its inner surface. It extends to the anterior border of the anterior testis. The main excretory tubules are ciliated for about three-fourths their length and reach from the anterior end of the vesicle almost to the acetabular level where each divides to form an anterior and a posterior collecting tubule. Each collecting tubule receives two secondary tubules, each of which is joined by the capillaries of two flame cells. The excretory formula remains unchanged during post-cercarial development. The flame cells are large, averaging 0.012 mm. in length.

Anisoporus manteri is compared with described species of *Anisoporus* in Table I. *A. manteri* differs significantly from *A. cobraeformis* in

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EXPLANATION OF PLATE II

(All figures concern *Anisoporus manteri*)

FIG. 7. Ventral view of an extended adult specimen (vitelline follicles omitted).

FIG. 8. Sagittal section of adult, showing junction of intestinal ceca and excretory vesicle.

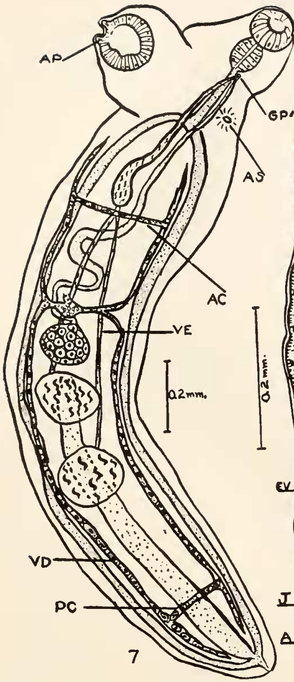
FIG. 9. Dorsal view of adult specimen.

FIG. 10. Details of reproductive system, drawn freehand from living specimen.

FIG. 11. Amphipod appendage containing five metacercariae.

ABBREVIATIONS

A, anus.
AC, anterior vitelline commissure.
AP, acetabular papillae.
AS, accessory sucker.
E, esophagus.
EG, egg.
EV, excretory vesicle.
GP, genital pore.
J, junction of ceca and excretory vesicle.
LC, Laurer's canal.
MG, Mehlis' gland.
OO, ootype.
OV, ovary.
PC, posterior vitelline commissure.
PH, pharynx.
PP, prepharynx.
SV, seminal vesicle.
U, uterus.
V, vitelline follicle.
VD, vitelline duct.
VE, vas efferens.
VR, vitelline reservoir.



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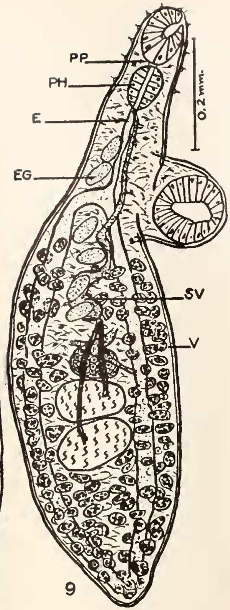

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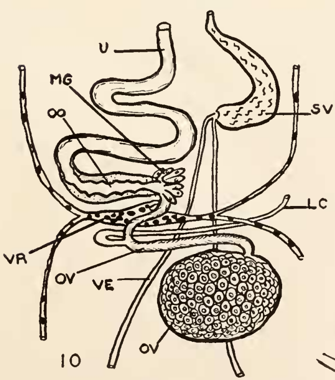

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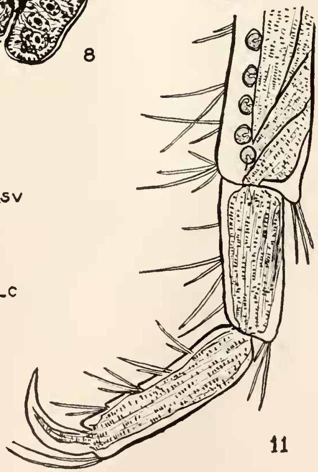

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PLATE II

size of body, suckers, testes, ovary and eggs, and the position of the genital pore. *A. eucinostomi* and *A. manteri* are similar in all respects except egg size and shape of the ovary. All three species differ widely in respect to host and locality.

Metacercaria (Figs. 3 and 5)

Metacercariae occur in the haemocoele throughout the body of the marine amphipods, *Carinogammarus mucronatus* (Say) (Fig. 4) and *Amphithoë longimana* Smith. Of 239 amphipods (143 *C. mucronatus* and 96 *A. longimana*) examined for natural infections, 10 per cent were

TABLE I

Comparison of Species of Anisoporus

Species	*A. cobraeformis* Ozaki, 1928	*A. eucinostomi* Manter, 1940	*A. manteri* Hunninen and Cable, 1940
Length (mm.)	4.3–7.2	1.222–2.497	0.74–2.32
Width (mm.)	0.33–.5	0.345–.465	0.28–.46
Oral sucker width (mm.)	0.16–.21	0.109–.144	0.07–.14
Ventral sucker width (mm.)	0.2–.28	——	0.12–.17
Ovary width (mm.)	0.13–.23	——	0.09–.14
Ovary shape	globular	subtriangular	ovoid
Ovary position	separated from anterior testis	close to anterior testis	close to anterior testis
Testes width (mm.)	0.16–.33	——	0.14–.2
Eggs length	0.044–.046	0.041–.048	0.062–.068
Eggs width	0.03–.033	0.025–.029	0.035–.04
Genital pore position	closer to ventral than to oral sucker	very close to pharynx	very close to pharynx
Locality	Japan	Galapagos Is.	Massachusetts, U. S. A.

positive. The number of cysts per amphipod varied from one to seven, averaging between two and three.

The encysted worm is folded on itself (Fig. 3) and closely surrounded by an elastic cyst membrane 0.004 mm. thick. The membrane is easily ruptured with a needle. The size and shape of the metacercaria depend on the age of the infection, young cysts being spherical and less than 0.15 mm. in diameter; older ones are ovoid and measure as much as 0.785 by 0.675 mm. In large cysts the worms become sexually mature and eggs are laid within the cyst. One metacercaria contained 24 eggs, most of which were free in the cyst fluid. These eggs measured 0.061–.66 (av. 0.064) mm. in length by 0.035–.39 (0.038) mm. in width and appeared to be as normal as those in worms removed from the definitive host.

Amphipods were easy to infect experimentally. In one group of 11 amphipods exposed for four days to cercariae, one was negative on examination while ten contained 4, 4, 7, 7, 8, 8, 13, 13, 15 and 17 small metacercariae, all of about the same size. In another experiment, 11 amphipods were exposed to cercariae for five days and found upon examination to contain 1, 1, 6, 7, 7, 10, 10, 12, 14, 28, and 334 cysts. Two amphipods in this group were naturally infected, one with two cysts and the other with one, all three being considerably larger than the metacercariae from experimental infections of the same amphipods. Exposure of amphipods to large numbers of cercariae results in heavy infections in which the cysts are found throughout the body, even in the antennae and legs (Figs. 4, 11).

In 2-day-old metacercariae (Fig. 3), the stylet is still present but is absorbed between the third and fourth days. Soon after encystment, the relatively long prepharynx of the cercaria begins to shorten so that in older metacercariae it is visible only when the body is extended. Dobrovolny (1939*b*) has described a similar shortening of the prepharynx in *Plagioporus lepomis* during post-cercarial development.

Cercaria (Figs. 1–2)

Specific Diagnosis.—Modified cotylomicrocercous type. Body contracted 0.12 long, extended over 0.325, average 0.225; cuticula aspinose; oral and ventral suckers lined with fine spines; a circlet of about 10 papillae with sensory "hairs" surrounding mouth. Tail extended 0.048–.056 long and 0.018 wide near base, moderately contracted 0.028–.039 long and 0.031 wide, filled with glands the ducts of which form a protrusible papilla. Oral sucker 0.035 long and 0.031 wide; stylet double pointed, 0.01–.011 long and 0.005 wide; prepharynx long and slender, pharynx 0.011 in diameter. Ventral sucker 0.032 in diameter. Three pairs of cephalic glands with a single lateral and two median ducts on each side. Oval excretory vesicle filled with granular masses. Main excretory tubules ciliated, dividing at level of acetabulum to form anterior and posterior collecting tubules. Excretory formula $2[(2+2)+(2+2)]$. Develop in sausage-shaped sporocysts with terminal birth pore.

Host.—*Mitrella lunata* (Say).

Locality.—Waquoit Bay, Cape Cod, Massachusetts, U. S. A.

The cercaria of *A. manteri* differs from described cotylomicrocercous cercariae in that the tail, instead of forming a hollow sucking cup, is filled with large gland cells which secrete a sticky substance. The tail becomes so firmly attached to objects that the cercaria is not dislodged by water currents of considerable force. In addition to extension and contraction of the body during the waving, exploratory, and inch-worm movements characteristic of most cotylomicrocercous cercariae, the larvae of *A. manteri* have a peculiar type of behavior, commonly observed in attached specimens. The extended cercaria loops on itself so that its shape is approximately that of the letter " e " written vertically. The body is then straightened with a sudden spiral movement. This coiling and uncoiling movement sometimes gives the illusion that the cercaria reverses ends.

Sporocysts of *A. manteri* occur in the branchial region and digestive gland of the snail. They are simple, sausage-shaped forms with a protrusible anterior end bearing the birth pore. The largest sporocyst measured was 0.65 mm. long and contained 35 apparently mature cercariae.

Discussion

The present study demonstrates that *Anisoporus* and probably the related genera *Opecoelus, Opecoeloides,* and *Opegaster* are co-familial with other trematodes having cotylomicrocercous cercariae and do not constitute a distinct family as maintained by Ozaki (1925, 1929). Hence, Odhner (1928) and Stunkard (1931) are supported in their opinion that anal openings in these trematodes are of significance only in the separation of genera and species.

If, in the phylogeny of the trematodes, convergent evolution has occurred, one would expect to find evidences of it in the parasites of fishes, the oldest class of vertebrates. Convergent evolution would account for similarity of adult stages of species having fundamentally different larvae as now well demonstrated in the Allocreadiidae. On the other hand, divergent evolution apparently has led to the separation of adults which appear to be distantly related but actually have similar larval stages. An excellent illustration is afforded by the separation of the Acanthocolpidae from the Allocreadiidae on the basis of spines in the cirrus and metraterm. According to Martin (1939), the acanthocolpid, *Stephanostomum tenue,* has an ophthalmoxiphidiocercaria while the authors (Cable and Hunninen, 1940) have found that another acanthocolpid, *Deropristis inflata,* has a trichocercous larva. Not only are these larvae dissimilar, but each displays characteristics common to certain members of the family Allocreadiidae. Hence a classification based on actual relationships will require the combination and reclassification of the Acanthocolpidae, Allocreadiidae, and possibly the Monorchiidae.

The task of reclassifying the group would be a formidable one and must evaluate both larval and adult characters with great care. Larval and particularly cercarial structures may actually be misleading in some cases, particularly in groups in which only a few life histories are known. The elimination of a free-swimming period during cercarial life is often accompanied by extreme reduction and even complete loss of the tail; such modification may occur even in cercariae which emerge from aquatic hosts. A good illustration is afforded by the brachylaemids whose cercariae were known until very recently only from pulmonate gastropods, many of which are terrestrial. In these hosts the tails of the cercariae are extremely rudimentary or lacking altogether. Recently, however, Allison (1940) has found in the prosobranch snail, *Campeloma,* a furcocercous brachylaemid cercaria which, as he states, strongly suggests a relationship between the Brachylaemidae and other trematodes having furcocercous cercariae.

When considered only as formulae, excretory systems also may be misleading, as exemplified by *Cercaria coronanda* Rothschild, 1938, the cercaria of *Exorchis oviformis* as described by Komiya and Tajimi (1940), and an undescribed species discovered by the authors, all of which are true pleurolophocercous cercariae but with an excretory formula of $2[(2+2)+(2+2)]$. This formula is the same as that of the microphallids but a consideration of other larval characteristics gives no reason to consider the cercariae mentioned as intermediate types between the pleurolophocercous larvae of the Opisthorchioidea and the xiphidiocercous larvae of the Microphallidae. It is clear that the excretory pattern must be correlated with other larval characteristics, all of which must be considered as a whole.

There are pleurolophocercous cercariae without eye-spots, cotylomicrocercous forms without stylets, microphallid larvae without tails, and strigeid fork-tails without pharynges. Yet other larval characteristics give definite clues to relationships.

Much has been accomplished by the study of adult material as indicated by the manner in which life-history studies have confirmed relationships postulated on the basis of adult morphology. Structure of adults may be the deciding factor in the classification of species having cercariae so modified that they might be considered either as aberrant members of some well-defined group or as a distinct larval type. For example, the cercaria of *Monorcheides cumingiae* (Martin, 1938) differs from typical trichocercous species in the nature of the tail and excretory pattern and may be a separate larval type. Determining the relationship of this species to other trematodes, and hence the validity of the family Monorchiidae, may depend as much on adult as larval characters, particularly until more than one life cycle in the family is known.

It is concluded that a revision of the Allocreadiidae is needed and at present could be proposed to the extent of defining families and placing certain genera in them. Even so, our knowledge of the morphology and life histories of many genera is so incomplete that their allocation to families would be a matter of conjecture.

We believe that the trematodes at present assigned to the family Allocreadiidae represent at least three distinct families, possibly belonging to more than one superfamily. This belief is justified if the heterophyids and opisthorchiids, with practically identical cercariae, are correctly regarded as separate families of the same superfamily.

Very recently, Hopkins (1941) has accepted the validity of the family Opecoelidae and included in it all allocreadoid genera having an excretory formula of $2[(2+2)+(2+2)]$, and cercariae of the cotylomicrocercous type. Leaving all other genera in the family Allocreadiidae, he includes in the Opecoelidae the genera *Cymbephallus, Podocotyloides, Enenterum, Dactylosomum, Coitocaecum, Genitocotyle, Nicolla, Ozakia,* as well as the more typical opecoelid genera *Opecoelus, Opegaster, Opecoeloides, Anisoporus,* and *Opecoelina.* Hopkins also implies but does not definitely state that *Helicometra, Plagioporus, Hamacreadium, Sphaerostoma,* and *Podocotyle* also should be included. Since Mathias (1937) has found that *Allocreadium angusticolle* has a cotylomicrocercous cercaria, the genus *Allocreadium* also should be included in the above group. Obviously, the name Allocreadiidae is available only for the family including the type genus *Allocreadium;* this genus must be regarded as co-familial with the genera Hopkins allocates to the family Opecoelidae. Either the name Allocreadiidae or Opecoelidae must be suppressed. Since Allocreadiidae is an older and more familiar name than Opecoelidae and Ozaki proposed the family Opecoelidae without knowledge of either excretory systems or life histories, but separated it from the Allocreadiidae on the basis of characters which have not been generally accepted as valid, it is proposed that the name Allocreadiidae take precedence over Opecoelidae. This proposal simply means that the family Allocreadiidae is restricted to include only those forms having cotylomicrocercous cercariae and a simplified excretory pattern. In any event, it will be necessary to propose new families or redefine existing ones to include the genera excluded from the restricted family. Such a revision is beyond the scope of the present paper.

Summary

The life history of *Anisoporus manteri* Hunninen and Cable, 1940, has been traced experimentally. The cercaria, a cotylomicrocercous type,

develops in sporocysts in the marine snail, *Mitrella lunata* (Say) and encysts in the marine amphipods, *Carinogammarus mucronatus* (Say) and *Amphithoë longimana* Smith. Old metacercariae contain eggs in the uterus and cystic fluid. Adult worms occur in the intestine of the marine fishes, *Syngnathus fuscus* Storer, *Paralichthys dentatus* (Linnaeus), *Hippoglossoides platessoides* (Fabricius), *Apeltes quadracus* (Mitchill), *Fundulus heteroclitus* (Linnaeus) and *F. majalis* (Walbaum).

It is proposed that the family Allocreadiidae be restricted to include only trematodes having cotylomicrocercous cercariae and simplified excretory patterns, since the type genus, *Allocreadium,* would be included in the restricted family. Consequently, the family name, Opecoelidae, would be suppressed as a synonym of Allocreadiidae *sensu stricto.*

Addendum and Correction

In respect to the uroproct, the present species is more like *Opecoeloides* than *Anisoporus.* Odhner (1928) erected the genus *Opecoeloides* to contain a single species, *Distomum furcatum* Bremser, and described in this form the union of the ceca with the excretory vesicle as has been observed in the present study. In *Anisoporus,* as defined by Ozaki (1928), instead of joining the excretory vesicle, the ceca unite posteriorly to form a median tube with an anal opening independent of the excretory pore. In other respects, the genera *Opecoeloides* and *Anisoporus* are identical. While the present paper was in preparation, the writers were inclined to share with Manter (1940) doubt as to the generic significance of the uroproct as well as sucker papillae, characters used extensively in the separation of genera. The paper in which Odhner proposed the genus *Opecoeloides* appeared Nov. 13, 1928, while Ozaki's definition of *Anisoporus* was published Dec. 31 of the same year. Whether or not these genera are regarded as synonymous, *Opecoeloides* is the older name and the present species must be placed in that genus; accordingly, the correct designation is *Opecoeloides manteri* (Hunninen and Cable, 1940). The species for which Odhner erected the genus has never been mentioned in the literature except as *Distomum furcatum;* its proper designation is *Opecoeloides furcatum* (Bremser in Rudolphi, 1819). The writers have been unable to find a satisfactory description of this species, but from Odhner's paper it is possible to differentiate *O. furcatum* and *O. manteri,* the only species in the genus, on the basis of sucker papillae; there are six in *O. furcatum* and five in *O. manteri,* three anterior and two posterior. Since the present study supports the observations of Odhner and adds a second species of *Opecoeloides,* the validity of the genus is strengthened considerably. It therefore seems advisable to maintain *Anisoporus* and *Opecoeloides* as distinct genera, particularly since proposing synonymy for them would cause a certain amount of confusion.

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